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Ecology of higher fungi in *Tsuga diversifolia* and *Betula ermani-Abies mariesii* forests of subalpine zone*

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Summary

A survey on fungal flora in subalpine mixed forest, and studies on the ecological characters of higher fungi and fungal communities in *Tsuga* and *Betula-Abies* stands were performed at Shiga Kogen, Nagano Pref. The fungal activity was depressed from November through May with snow, freezing and the excess of water. The fungal species collected were 121 including 62 mycorrhizal fungi and 57 saprophytes. As for mycorrhizal ones, the frequency of *Gomphidius tomentosus*, *Hygrophorus hypothejus*, *Rozites caperatus* and *Cortinarius mucifluus* was high in *Tsuga* stand, and that of *Amanita* and *Russula* in *Betula* stand. Dominant species among saprophytes were *Mycena vulgaris* and some *Collybia* species. The species composition in *Tsuga* stand was perfectly different from that in *Betula-Abies* stand. Fungi with various kinds of life type inhabited in *Tsuga* stand, but those in *Betula-Abies* stand belonged to the rhizomorph former. The occupied area by fungi was 42% of the plot in the former and 62% in the latter. The species number of mycorrhizal fungi was more in *Tsuga* stand than in *Betula-Abies* stand. The differences of the species composition, distribution, dominant species and their life types between two stands were caused by the differences of the vegetation, root distribution, the composition of organic matter and humidity.

Introduction

The microbial community in forest ecosystem can be characterized by the abundancy of higher fungi, mainly Basidiomycetes and Ascomycetes, comparing with those in other ecosystems, grassland and cultivated field. Actually their abundancies can be recognized by the fruit body production and the existence of visible mycelia in surface soil in field.

These higher fungi are classified, in general, into three major groups according to their ecological characters; symbiont—mycorrhizal fungi, saprophyte—litter and wood decomposer and parasite—parasitic against plants and animals.

On the other hand, most of higher fungi are able to survive for longer term in soil

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or in their substrates forming mycelial mat, colony, mycelial strand or rhizomorph which can protect themselves against feeders or parasites and endure even under severe climatic conditions. They can also form their own territories depending on the ability to produce some relatively united mycelial structures and to repel the other microorganisms from their territories (Warcup 1951, Ohara 1968, Ogawa 1976). These fungal territories are not only competing or coordinating with each other among them but also affecting to other soil microorganisms and animals directly or indirectly (Ogawa 1969).

Generally the forest has offered the suitable conditions for the survival of higher fungi through the constant supply of various kinds of substrates and relatively stable physical conditions without strong disturbances, and higher fungi themselves also have evolved in it adapting to a stable but complex ecosystem.

Higher fungi playing various ecological roles as one of the important components in forest ecosystem should be investigated and can be utilized in order to apprehend the microbial community in forest macroscopically, although they are apt to be neglected in the field of microbial ecology or soil microbiology.

It has been well known that the distribution of microorganisms in forest soil is irregular depending on the surroundings and specific characters for microorganisms themselves. The behaviors of higher fungi in soil are pretty different from those of other soil microbes, and most of them are growing in soil forming some developed mycelial structures like rhizomorphs and hyphal strands or the perennial colonies in large scale.

Substrates for microorganisms distribute irregularly over forest floor because of ununiform distribution of plants and soil conditions resulting from uneven topography. The quantity and quality of litter also vary even in small area. Therefore, most of saprophytes have also distributed ununiformly reflecting the variety of substrate distribution. The distribution of symbionts and parasites has been ruled by that of plant. From the view points of microorganisms, it seems to be essential for the investigation of ecology of higher fungi that a certain forest ecosystem should be divided into several subecosystems depending upon soil conditions and plant communities in it.

I. Environments in the research area.

The research area situates at Shiga plateau, elevation 1500–1800 m, in Nagano Pref.. Research stand was settled in the flat with rugged topography on the flank of Mt. Shiga. There were a lot of mounds and hollows over the flat which consisted of lava and andesite being covered with volcanic ash.

Annual average temperature was 5.3 C, average temperature in summer season below 20 C, and that from the end of November through the end of April below 0 C. Annual total precipitation reached to 1800–2000 mm, and snow fall began at the be-

gining of November and ended at the end of April in normal years. Snow fall attained about 2.5 m on the flat in February, and this area was covered with snow for almost six months. Melting snow remained until the end of May on the hollows. So this forest was so humid through a year (Mitsudera 1970).

Tsuga diversifolia, Abies mariesii and *Betula ermani* are dominant in this area, but *Larix leptolepis* and *Thuja standishii* occupied some places. *Rhododendron metternichii, R. metternichii* var. *degronianum, R. molle, R. albrechti, Acer ukurunduense* and *Sasa kurilensis* are dominant as the understory vegatation with several kinds of grass and herbs. Most of forest floor is covered by mosses or bumboo shrubs. The species compositions of understory vegetation vary with the differences of dominant tree species and soil conditions.

In this area most of places are covered with black, dark brown or podsolic soils, but several varieties of them develop in small scales being caused from irregular topography. Four major soil types were reported in the research area (Kurotori 1968); B_D, wet brown forest soil, subalpine type. P_D, dry podsolic soil with thin bleached zone, A_2 horizon. $P_W(h)$, wet podsolic soil with iron accumulation in B_2 horizon and with B_1 horizon rich in humus. $P_W(i)$, wet podsolic soil with grayish brown A_1 horizon, grayish white and bleached A_2 horizon, and ion pane below A_2 horizon. Hydrogen ion concentrations in A_1 horizons were pH 3.3 to 3.8 and those in A_2 horizons pH 4.0 –4.5 on these soils.

This area could be subdivided into several sites by the soil type, vegetation, understory vegetation and topography correlated mutually through the development of the forest ecosystem. There was *Tsuga-Abies* stand on the tops of small mounds with dry podsolic soil, P_D, and the forest floor was covered with thick layer of mosses. The soil and soil organic matter layer were relatively dry including a number of roots and decaying woods. The density of *Tsuga* with the depressed height growth was comparatively high mixing with the saplings of *Abies*. At the foots of small mounds and the slope with wet podsolic soil, $P_W(i)$ or wet brown forest soil, B_D, *Abies* grew as a dominant species with bamboo shrub and *Betula* saplings. *Betula* stand with grass and herbs developed over the flat or gentle slopes with wet brown forest soil, subalpine type, B_D or wet podsolic soil, $P_W(h)$, with humus accumulation. *Abies* and *Betula* stands were covered by snow for longer term than *Tsuga-Abies* stand and often filled with water of melting snow in spring.

The studies on the soil microbial flora and their functions in this area were reported in the series of internal reports of JIBP (Kitazawa, ed., 1968, 1969, 1970, 1971, 1972, 1973).

II. Higher fungi occurring in the research area.

Sporocarps of higher fungi were collected from May through October in 1969 and

Tab. 1 List of higher fungi in *Tsuga diversifolia*, *Abies mariesii* and *Betula ermani* forests of subalpine zone. Shiga yama, Shiga plateau, Nagano Pref. Sporocarps were collected through summer and fall in 1968, 1969 and 1970. Ecological characters were classified into three major groups depending on the field observation; S: saprophyte, S–M: mycorrhizal fungi with saprophytic character, M: mycorrhizal fungi (obligate mycorrhizal fungi).
S, 57 species. S–M, 42 species. M, 20 species.

M	*Hygrophorus hypothejus*	S–M	*Pulveroboletus ravenellii*	S	*Lepiota* sp.
S	*H. leucophaeus*	S–M	*Leccinum scabrum*	S	*Lepiota* sp.
S	*H. pseudococcineus*	S–M	*L. aurantiacum*	S–M	*Gomphidius rutilus*
S–M	*Hygrophorus* sp.	S–M	*Tylopilus neofelleus*	M	*G. tomentosus*
S	*Collybia maculata*	S–M	*T. felleus*	S–M	*Gomphidius* sp.
S	*C. dryophila*	S–M	*Aureoboletus cramesinus*	M	*Inocybe kobayasii*
S	*Collybia* sp.	M	*Suillus* sp.	M	*Inocybe* sp.
S	*Mycena galericulata*	S–M	*Lactarius camphoratus*	M	*Inocybe* sp.
S	*M. galopus*	S–M	*L. chrysorrheus*	S–M	*Laccaria laccata*
S	*M. haematopus*	M	*L. nigroviolascens*	S–M	*L. proxima*
S	*M. epipterygia*	M	*L. lignyotus*	S	*Stropharia hornemannii*
S	*M. alcalina*	S–M	*L. vellereus*	S	*S. aeruginosa*
S	*M. vulgaris*	S–M	*L. piperatus*	S	*Gymnopilus spectabilis*
S	*M. pura*	M	*L. glyciosmus*	S	*G. penetrans*
S	*Mycena* sp.	S–M	*Lactarius* sp.	S	*Cortricia cinnamomea*
S	*Marasmius purpureostriatus*	S–M	*Russula pseudodelica*	S	*Hebeloma* sp.
S	*M. siccus*	S–M	*R. aurata*	S	*Hebeloma* sp.
S	*M. ramealis*	S–M	*R. solaris*	S	*Pleurocybella porrigens*
S	*M. perforans*	S–M	*R. senecis*	S–M	*Cantharellus tubaeformis*
S	*Marasmius* sp.	S–M	*R. foetens*	S–M	*Cantharellus* sp.
S	*Marasmius* sp.	S–M	*R. emetica*	S	*Clavariadelphus pistillaris*
S	*Oudemansiella mucida*	S–M	*R. sanguinea*	S	*Clavulinopsis miyabeana*
S	*Tricholomopsis platyphylla*	S–M	*R. crustosa*	S–M	*Ramaria* sp.
M	*Amanita muscaria*	S–M	*R. cyanoxantha*	S	*Paxillus panuoides*
M	*A. caesarea*	M	*Cortinarius turmalis*	S	*Leotia lubrica*
M	*A. pantherina*	S–M	*C. semisanguineus*	S	*L. lubrica* f. *aurantipes*
M	*A. vaginata*	S–M	*C. watamukiensis*	S	*Cordyiceps capitata*
M	*A. pseudoporphyria*	S–M	*C. hinnuleus*	S	*C. japonica*
M	*A. virosa*	S–M	*C. armillatus*	M	*Elaphomyces granulatus*
M	*Amanita* sp.	S–M	*C. variicolor*	S	*Scutellinia scutellata*
S	*Amanita* sp.	S–M	*C. pholideus*	S	*Helvella macropus*
S	*Pholiota lubrica*	S–M	*C. mucifluus*	S	*Bulgaria inquinans*
S	*P. spumosa*	S–M	*C. flexipes*	S	*Craterellus cornucopioides*
S	*Pholiota* sp.	S–M	*Cortinarius* sp.	S	*Cantharellula umbonata*
S–M	*Boletus edulis*	S–M	*Rozites caperata*	S	*Telephora palmata*
S–M	*B. rubellus*	S	*Rhodophyllus acutoconicus*	S	*Trichoglossum hirsutum*
M	*B. pulverulentus*	S	*R. crassipes*	S	*Tremella* sp.
M	*B. erythropus*	S	*R. coelestinus*	S	*Macrocystidia cucumis*
S–M	*Boletellus mirabilis*	S	*Rhodophyllus* sp.		
S–M	*Boletus* sp.	S	*Lepiota lutea*		

from July through September in 1970 once or twice a month periodically. The mycelial structures in soil and substrates were detected in field and ascertained under microscopes. Their functional characters were classified into three major groups; S: saprophyte, M: mycorrhizal symbiont and S–M: mycorrhizal fungi being supposed to have slight saprophytic activities, facultative mycorrhizal fungi.

Fungal species collected from this research area are listed up in Tab. 1.

Sporocarp production started at the beginning of May just after snow melting with the appearance of *Tremella* sp., *Helotium* sp. and *Bulgaria* sp.. Species compositions and productivities in each season varied depending on climatic conditions, mainly temperature and precipitation. In midsummer *Russula, Hygrophorus* and Boletaceae became dominant, and in fall *Mycena, Collybia, Cortinarius, Amanita, Russula* and *Lactarius* produced their fruit bodies abundantly. The production of sporocarps finished with *Mycena vulgaris* and *Hygrophorus hypothejus* at the end of October when it began to freeze and snow.

The final fungal activities on newly fallen leaves and needles were observed in October. The mycelial strands of *Mycena vulgaris* and another unidentified species protruded numerously from the old decomposed leaves of *Betula* and then fixed the fresh fallen leaves to the ground. After being fixed the color of leaves changed to whitish yellow according to the enlargement of colonies over the underside of leaves. In *Betula* stands, these fine mycelial strands covered mostly all over the grounds. These mycelia on the leaves were activated in wet chamber under low temperature below 5 C and could be isolated on the medium with the leaf extract. The newly fallen needles of coniferous trees were also fixed by several kinds of hyphae coming out of old decaying needles, but their reproductive organs could not be identified in field. Saito *et al.* (1970, 1971) reported on the litter decomposing fungi in detail.

The growth of some mycelial strands or rhizomorphs and the reformation of mycorrhizae were observed even under melting snow in early spring. The apparent microbial activities seemed to be restricted only for six months here and depressed for other term because of heavy snow and freezing of ground surface.

Total species number collected were 121 among which the saprophytes were 57 and mycorrhizal ones 62. The mycorrhizal fungi were dominant with high productivities of sporocarps and occupied comparatively large area, because all of the three dominant tree species were ectomycorrhizal plants.

Saprophytes decomposing needles, leaves, woods and so on were abundant in L, F layers and decaying woods. *Mycena vulgaris, Mycena* spp. and *Marasmius* spp. were enlarging their colonies forming mycelial strands or rhizomorphs over fresh litters and twigs. For instance, the amount of black hard rhizomorph of *Marasmius* sp. reached to 0.5–0.8 g in 10×10 cm square in *Betula* stand. *Collybia maculata* and some other species of *Collybia* formed thick mycelial mats and decomposed leaf litter. They seem to be lignin decomposers because of white rot. In humus layer at coniferous stand, *Leotia*

and *Hygrophorus* species formed the mycelial mats and conjugated soil particles tightly.

Obligate mycorrhizal fungi were 20 including the species belonging to the genera *Amanita, Hygrophorus, Gomphidius, Cortinarius, Lactarius, Inocybe* and *Elaphomyces*. These fungi with developed rhizomorphs or small mycelial mats inhabited massively in F or FH horizons forming pinnate or coralloid mycorrhizae. *Hygrophorus hypothejus* and *Gomphidius tomentosus* which were dominant species in *Tsuga-Abies* stands formed big clusters of coralloid mycorrhizae with a lot of branches and developed rhizomorphs. *Amanita* species which were abundant in *Betula* stands had fine developed rhizomorphs with specific morphological features for each species and formed numerous fine pinnate mycorrhizae on *Betula* roots. The sporocarps of *Elaphomyces* were produced in humus layer being covered by ectoendo-mycorrhizal net and sometimes parasitized by *Cordyceps capitata*.

The facultative mycorrhizal fungi were 42 species. These fungi belonging to the genera *Hygrophorus, Russula, Laccaria, Suillus, Cortinarius, Cantharellus* and *Ramaria* inhabited in the surface layer of mineral soil rich in organic matters. Most of them formed merely the undeveloped mycelial strands or large mycelial mats and rod or pinnate mycorrhizae dispersedly. *Rozites caperata* and *Cortinarius mucifluus* formed the gray and thick mycelial mats in F layer with high moisture content and ectomycorrhizae or pseudomycorrhizae on the root of *Tsuga* and *Abies*. *Boletus* and *Suillus* inhabited in F layer forming densely undeveloped mycelial strands and small pinnate mycorrhizae on the roots of conifers.

In general, *Cortinarius, Hygorphorus, Tricholoma, Inocybe* and *Elaphomyces* were abundant in coniferous stands, and *Cortinarius, Amanita, Russula, Lactarius* and some of Boletaceae in *Betula* and mixed stands in this area. The production of sporocarps in subalpine forests seems to be higher than those in other forests at low altitude.

III. Fungal communities in *Tsuga diversifolia* and *Betula ermani-Abies mariesii* stands.

Methods

Mapping method was applied to investigate the fungal community, substrates for microorganisms and other environmental factors in detail. After the survey on fungal flora, two representative sites were selected at the places without bamboo shrubs, and the quadrates with 2×2 m unit squares, plot 1 and 2, were settled there. Plot 1, 6×8 m square, where *Tsuga diversifolia* was dominant mixing *Abies mariesii* saplings situated from the top to the flank of small mound with P_D type soil. Plot 2, 6×6 m square, where *Betula ermani* was dominant with scarce understory vegetation mixing a few *Abies* situated on the humid flat with P_W(h) type soil.

1. Substrates for microorganisms.

Soil profiles were surveyed by usual trenching method at each representative site. Soil organic matters and roots were sampled near by plots 1 and 2 according to soil horizons by means of 30×30 cm square frame. Components of L layer were divided into several fractions, moss, twig, leaves or needles and so on. The substances in F and H layers were fractionated by sieves with 3.5, 10 and 16 mesh after desication, and then the fractions which were acertained to belong to the same stages of decomposition were mixed together as one fraction even though a part of it originated from other layers (Ogawa 1973).

In this study humic substances mixed with mineral soil were neglected. Root and mycorrhiza were extracted from the samples of F and H layers by hand and washed on the sieves. The amount of mycorrhizae was estimated by subsample including soil organic matters under microscope. Mycelial mats or crusts were estimated after taking out roots and organic matters (Ogawa 1973).

Decaying woods covering the ground or being buried in soil and stumps were detected and mapped, and the covering area of them were estimated after mapping.

2. Fungal territories and their ecological characters.

All the higher fungi occurring in the quadrates were collected once or twice a month from the begining of August through the middle of November in 1970. Their dry weights were estimated after identification. The occurring positions of sporocarps were marked by pegs in field and recorded on the maps. The ecological characteristics of each fungus were examined in field especially on mycorrhizae, mycelia in soil, habitats, substrates and so forth. After the studies on their ecological characters, their presumed territories were drawn on the maps referring to the occurring positions, mycelial structures and habitats. And the occupied areas were measured from the maps.

Results and discussion

1. Substrates for microorganisms.

a) Soil organic matters and litter.

Soil profiles distributing near by plots 1 and 2 are shown in Fig. 1. The features on profiles are described previously. P_D type soil distributed around plot 1, and $P_W(h)$ type soil around plot 2. On the profile of P_D in *Tsuga-Abies* stand, gray mycelial mat of *Cortinarius mucifluus* was characteristic containing a lot of pinnate type mycorrhiza, and there was formed the gap between mycelial layer (MH horizon) and HA horizon. A_0 horizon could be divided into five layers, but the samples for estimation of amount were taken from three layers. The surface, L layer with 1–2.5 cm thick, was covered

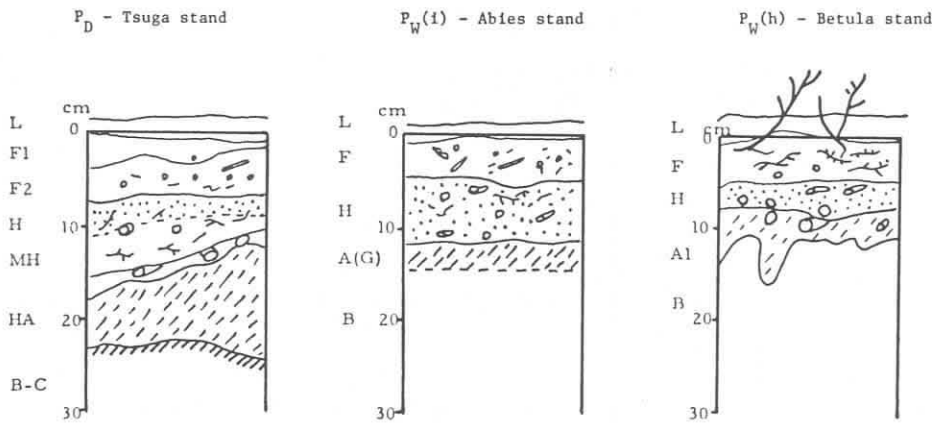

Fig. 1. Representative soil profiles observed near the research plots. L, F, H, MH, A_1, A(G) and B–C: soil horizons. P_D; dry podsolic soil. P_W(i): wet podsolic soil, ion accumulation type. P_W(h): wet podsolic soil type, humus accumulation type. The explanation of these profiles and the relations among soil types, vegetations and topography are described in the text.

by mosses, twigs and needles, and the total amount was 154 g in 30×30 cm square as shown in Tab. 2. F layer consisting of the fragments of twig, decaying needles and their fragments was 6–8 cm thick and 393 g. MH layer including roots, mycelium and the mycelial fragments mixing with humus was 5–10 cm thick and 1014 g.

On the profile of P_W(h) in *Betula* stand around plot 2, the surface was covered by *Betula* fallen leaves with 2–3 cm thick, and the twigs of *Betula* were bounded with numerous black rhizomorphs. In F layer the amount of undecomposed bark and twigs increased and was 299 g. The development of A_1 layer was recognized below H layer irregularly. The underward translocation of humic substances was characteristic comparing with those on other profiles.

On the profile of P_W(i) in *Abies* stand, L layer consisted of mainly *Abies* needles was 1–2.5 cm thick and 117 g. F layer was 5–7 cm thick and 615 g. The amount of undecomposed needles was more abundant than in P_D soil. The decomposition of organic matters seemed to be retarded because of high moisture content in soil. H layer being formed below F layer was 6–8 cm thick.

Sum total weight of organic matters including roots was 1561 g in *Tsuga* stand, 1722 g in *Abies* stand, and 674 g in *Betula* stand. In all of these stands, organic matters were accumulated over mineral soil densely, and their decomposition seemed to progress more slowly than that at low altitude.

The decomposition patterns in these three stands are shown in Fig. 2. The patterns in *Tsuga* and *Abies* stands exhibited the similar trends, but the decomposition of *Abies*

Table 2. Litter and roots in the surface soil of research plots. July, 1970.

Litter and roots were sampled by 30×30 cm frame from the ground surface according to soil layers. Roots were extracted from soil organic matters by washing, and mycorrhizae were cut off from the mother roots. Soil organic matters in F and H layers were divided into several stages of decomposition by means of sieving method after desiccation. Decomposition patterns of them are shown in Fig. 2.

	Sampling sites								
	1 *Tsuga diversifolia* stand P_D type soil			2 *Abies mariesii* stand P_W(i) type soil			3 *Betula ermani* stand P_W(h) or B_D type soil		
Layers	Depth cm	Fractions	Dry weight g.	Depth cm	Fractions	Dry weight g.	Depth cm	Fractions	Dry weight g.
L	1–2.5	Moss	14	1–2.5	twig	36	2–3	twig	12
		Betula leaves	2		*Betula* leaves	3		bark	11
		twig	82		needles	39		*Betula* leaves	26
		needle	40		fragment	39		fragment	14
		fragment	5					others	6
		others	11						
		Total	154		Total	117		Total	69
F	6–8	root	35	5–7	root	9	4–5	root	27
		−3.5 mesh	88		−3.5 mesh needle	63		−3.5 mesh leaves	111
		3.5–10, needle	79		−3.5 mesh fragment	177		3.5–10, fragment	116
		10–16, fragment	71		3.5–10, fragment	188		10–16, fragment	39
		10–16, needle	50		10–16, fragment	96		16–	60
		16–	105		16–	91			
		Total (root)	393(35)		Total (root)	615(9)		Total (root)	326(27)
H	(MH) 5–10	root (rot)	136(39)	6–8	root	74	3–4	root	55
		mycelial crust	370		humus	990		−3.5 mesh	73
		mycelial fragment	605					3.5–10	108
								10–	98
		Total (root)	1014(136)		Total (root)	990(74)		Total (root)	279(55)
		Sum total (root)	1561(171)		Sum total (root)	1722(83)		Sum total (root)	674(82)

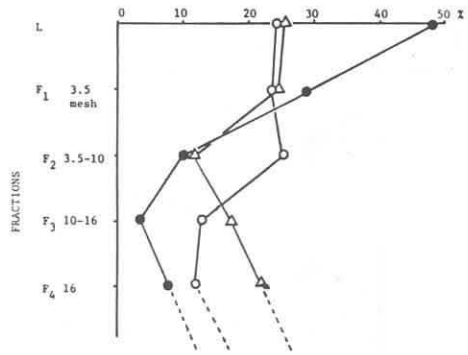

Fig. 2. Decomposition patterns of litters in *Tsuga diversifolia, Abies mariesii* and *Betula ermani* stands.

Samples of A_0 layer were collected from the representative sites in each stand according to sub-layers, L, F and H. After desiccation, each sample was divided into four or five fractions by means of sieves with different size fitful to the mechanical fragmentation of litter, and then they were classified into five grades depending on the morphological similarity under microscope. Percentages of each fraction to total weight of organic matters were shown in this figure.

needles seemed to be delayed on the stage from L to F_2 fraction comparing with the case in *Tsuga* needles. The decomposition process of *Betula* leaves progressed without retard as in the case of broad leaves at low altitude (unpublished). It was supposed that the differences among the decomposition patterns reflected the specificities of species composition of litter decomposers in each stand. Fungal species composition on leaves and needles was also specific for plant species (Saito 1970).

The accumulation of humic substances, fine particles, was remarkable in all stands. Such delay of decomposition probably resulted from poorer microbial flora and shortness of the term with high microbial activity. Chemical degradation of litter and the distribution of soil microbes on the profiles were reported by Takai *et al.* (1972, 1973).

The distribution of fine roots in surface varied depending on humidity, the amount and state of piled litter and physical properties of soil. In this area mycorrhizae distributed only in A_0 horizon, and most of fine roots were covered by fungal sheath.

b) Mycorrhiza and root.

The amount of root in P_D soil was 35 g in F layer and 136 g in MH layer. Fine roots in F layer were mycorrhizal ones including typical pinnate and coralloidal mycorrhizae. In MH layer there were recognized a lot of decaying mycorrhizae. Withering roots and root fragments mixing with mycelia and mineral soil were removed from the estimation. The amount of mycorrhizae was 22 g including several types.

The amount of roots in P_W(h) soil was 82 g in F and H layers, and that of mycorrhizae was 12 g in F layer. Most of fine roots grown in F layer bear numerous mycelial strands

and rhizomorphs. There were only old and larger roots in H layer. The amount of bamboo roots was 27 g in F and H layers.

The total amount of roots in $P_W(i)$ was 83 g, and the formation of mycorrhizae was observed only in F layer. Their amount was 8 g. There were few roots in horizons below A_0 layer, and the growth of roots in deeper horizons had been depressed with subterranean water.

Such distribution of tree roots and their densities affect species composition and fungal distribution specially of mycorrhizal ones. And the decaying roots and living roots seem to be utilized ceaselessly by microorganisms as an important substrate.

c) Decaying wood.

There are abundant decaying woods, logs, branches, roots and stumps in the natural forest without human disturbance. They are not only utilized by microorganisms and animals as their substrate, but also contribute to the regeneration of coniferous trees in subalpine forests.

These decaying woods could be classified to five stages according to the grade of the decomposition (Ogawa 1973). The first stage burying deeply in soil and being covered with moss consisted of the reddish brown fragments of wood, and the high moisture content and the high hydrogen ion concentration were kept even through dry season. The microbial population was also very poor, and some mycorrhizae and growing roots of *Abies* and *Tsuga* were observed in the heart wood in this stage. *Abies* saplings grew on the wood in lines.

The heart wood in the second stage being covered with mosses was not decomposed yet, but the outer parts were softened by wood decaying fungi. Saplings and seedlings of coniferous trees grew over the old logs in this stage. The microbial flora was also poor, and the hydrogen ion concentration was below pH 4.0. The moisture content was higher than that in the first stage.

Sporocarps of wood decaying fungi and seedlings of *Tsuga* were growing on the wood in the third stage where the surface of wood were decayed partly and covered with mosses. The microbial flora became rich in this stage.

The wood in the fourth stage was almost intact being covered with bark, but the part below bark began to be decayed, and that in the fifth stage was more intact than in the former stage. The wood fallen on the ground seems to remain without visible decay for a few years after falling.

The stages of decomposition and the features in each stage vary depending upon the kinds of tree. The example described above is that in *Tsuga* wood. Most of trees, in general, are attacked by fungi in heart wood at first, then fall to the ground and will be decomposed taking long time.

The distribution of decaying woods is drawn in Figs. 3 and 4. The areas covered with old logs and stumps reached to 23% of plot 1 in *Tsuga-Abies* stand, and 35% in

Betula stand. It can be prospected that the decaying wood, root and stump hold unique fungal florae in soil or on the ground and affect also the distribution of soil microbes.

It is probable that these decaying woods are offering the suitable conditions for the growth of saplings of conifers with ectomycorrhizae, because these woods are acidic and humid through a year with poor microbial florae. In fact, the fine roots of *Tsuga* and *Abies* in the wood of the first and second stages were perfectly covered with the fungal sheaths of *Cenoccocum* and some Basidiomycetes.

2. Fungal territories and their ecological characters.

Higher fungi occurring in plots 1 and 2 and their ecological characters are listed up in Tab. 3, and their occurring positions and territories were drawn on the maps in Figs. 3 and 4. Explanation of marks on the ecological characters is described in Tab. 3. The details on the ecology of each fungus will be reported later.

a) *Tsuga diversifolia-Abies mariesii* stand, Plot 1.

The species collected from this plot was 17, the number of sporocarps except for those of *Mycena* and *Marasmius* 254, and their total dry weight 168.4 g. The numbers of sporocarps of *Leotia lubrica, Lactarius chrysorrheus* and *Gomphidius tomentosus* were more than 45, but the number of sporocarps did not proportion to the dry weights. On the weight, *Russula solaris, Gomphidius tomentosus, Boletellus mirabilis* and *Elaphomyces granulatus* exceeded 20 g. So far as concerning to the number of sporocarps and the dry weight, *Gomphidius tomentosus* and *Lactarius chrysorrheus* were dominant species in this plot. On the other hand, the occupied areas of higher fungi which were calculated from the map reached to 42% of the plot. The large ones among them were those of *Mycena vulgaris, Russula solaris, Lactarius chrysorrheus* and *Gomphidius tomentosus.*

Mycena vulgaris was a litter decomposer inhabiting on the fresh fallen needles and widespread over the plot. *Russula solaris* seemed to be mycorrhizal fungus with the ability to utilize soil organic matter. This fungus enlarged its territory forming the white rhizomorph. *Lactarius chrysorrheus* was also mycorrhizal fungus forming wet and thick mycelial mat in F layer. *Cortinarius mucifluus* and *Rozites caperata* exhibited the similar life type to that of *Lactarius chrysorrheus. Gomphidius tomentosus* was characterized by the big cluster of white and coralloidal mycorrhiza, and its sporocarps occurred from the mycorrhizal mass. *Hygrophorus hypothejus* showed similar life type. So the occupied areas of these two species were narrower in spite of the abundancies of sporocarps comparing with others.

In plot 1 the percentage of mycorrhizal fungi was 70%, and that of the saprophytes was only 23%. Inhabitants in F or FH layer were 12, and those in other layers were each 2. Rhizomorph or mycelial strand formers were 41% of total species number, the formers of mycelial mat or large colony 35%, and the small colony formers 24%. Most of mycorrhizal fungi formed their pinnate or coralloidal mycorrhizae on the roots of

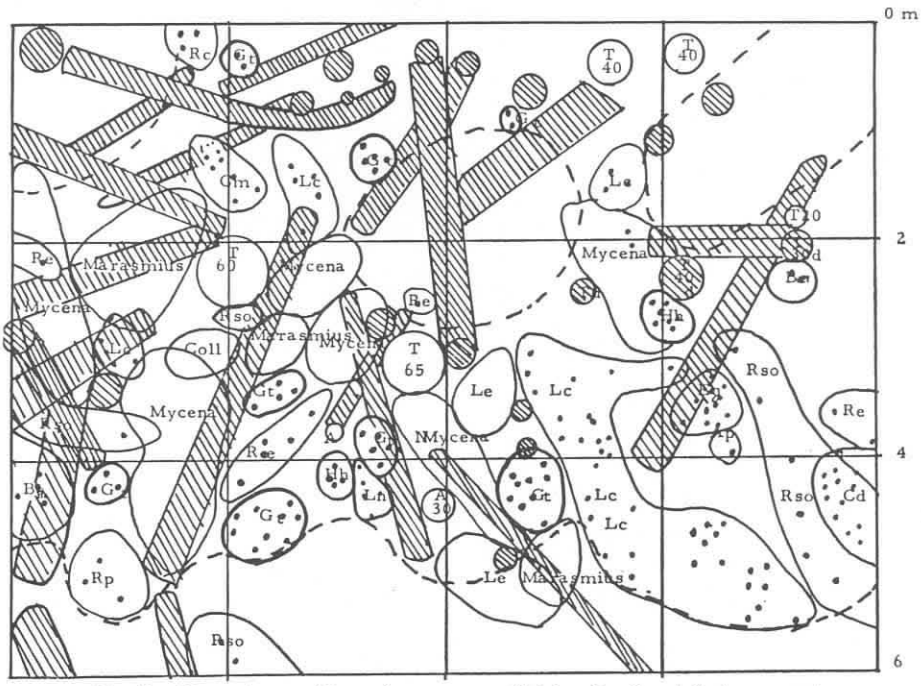

Fig. 3. Occurring positions of sporocarps of higher fungi and their apparent occupied areas in *Tsuga diversifolia* stand.

Sporocarps of higher fungi were collected from plot 1 from the beginning of July to the end of October in 1970 once or twice a month. Dots are the occurring positions. Apparent occupied areas are circled by lines. Zones covered with snow until the end of May are circled by dotted lines. Fungal species names and their marks are listed up in Table. 3. T: *Tsuga diversifolia* and A: *Abies mariesii* with the breast height diameter in cm.

Tsuga or *Abies,* but *Russula solaris, R. emetica* and *Amanita pantherina* formed them on the root of *Betula* which was invading into the plot.

The total of fungal territories was relatively narrow in plot 1 because of the uneven topography, and the territories of each fungus were duplicated or triplicated among the fungi with different life types or habitats because of the thick pile of organic matters. There were few occurrence of sporocarps at the hollow or the foot of mound where snow had remained until the end of May.

Comparing with the fungal flora in *Tsuga-Abies* forest along eastern coast of Honshu where the precipitation and humidity are lower than those in this area, the species composition in this area was perfectly different from that in the former area being characterized by the formation of wet mycelial layers in F layer and the absence of *Calodon* and *Tricholoma* which were dominant in dry subalpine coniferous forests (unpublished).

b) *Betula ermani-Abies mariesii* stand, Plot 2.

The species collected from plot 2 were 14, the number of sporocarps 167, and the

Table 3. Ecological characters of higher fungi occurring in plots 1 and 2.

Sporocarps of higher fungi were collected from the begining of July to the end of October in 1970. Plot 1: *Tsuga diversifolia-Abies mariesii* stand, 48 m². Plot 2: *Betula ermani-Abies mariesii* stand, 36 m². Marks of species names are applied in Figs. 3 and 4. The species with black point before the mark are common ones to both stands. S; saprophyte, S-M: mycorrhizal fungi

Plot 1 *Tsuga diversifolia-Abies mariesii* stand

Marks	Species name	Sporocarp		Function and substrate	Occupied area m²
		number	dry weight g.		
Mv	*Mycena vulgaris*	—	—	S litter	5.32
Ma	*Marasmius* sp.	—	—	S litter	1.71
●Le	*Leotia lubrica*	52	1.0	S humus	1.03
●Rso	*Russula solaris*	12	37.5	S-M root litter	2.98
●Re	*R. emetica*	8	1.6	S-M root litter	0.84
Rp	*R. pseudodelica*	3	9.6	S-M root humus	0.48
Lc	*Lactarius chrysorrheus*	55	16.5	S-M root humus	3.90
Ln	*L. nigroviolascens*	6	2.4	M root	0.13
Hh	*Hygrophorus hypothejus*	10	1.6	M root	0.30
Gt	*Gomphidius tomentosus*	45	20.3	M root	1.54
Rc	*Rozites caperata*	3	5.8	S-M root humus	0.15
Cm	*Cortinarius mucifluus*	7	5.0	S-M root humus	0.33
Bm	*Boletellus mirabilis*	5	34.7	S-M root humus	0.64
Ap	*Amanita pantherina*	1	3.0	M root	0.07
Eg	*Elaphomyces granulatus*	15	22.5	M root	0.30
Cc	*Cordyceps capitata*	10	1.8	P *Elaphomyces*	—
Cd	*Collybia dryophilla*	22	5.1	S wood	0.49
Total	17 species	254	168.4	S4, S-M7, M5, Pl	20.18

Plot 2 *Betula ermani-Abies mariesii* stand

Me	*Mycena epipterygia*	11	0.7	S litter	0.25
My	*Mycena* sp.	12	0.2	S litter	0.83
Agro	*Agrocybe* sp.	8	1.7	S humus	1.33
Mh	*Mycena haematopus*	6	0.1	S wood	0.17
Coll	*Collybia* sp.	2	1.8	S wood	0.07
●Le	*Leotia lubrica*	46	1.3	S humus	1.49
Rs	*Russula senecis*	42	138.0	M root	12.16
●Rso	*R. solaris*	3	10.0	S-M root litter	0.62
Ra	*R. aurata*	19	14.6	S-M root humus	2.09
●Re	*R. emetica*	5	1.2	S-M root litter	0.84
Tp	*Telephora palmata*	5	2.5	S humus	0.64
Av	*Amanita virosa*	4	12.2	M root	1.21
Ava	*A. vaginata*	3	14.0	M root	0.76
Tf	*Tylopilus felleus*	1	0.2	S-M root litter	0.11
Total	14 species	167	198.5	S7, S-M4, M3	22.57

with saprophytic activity, M: mycorrhizal fungi, P: parasite. L, F, F-H and H mean soil layers where the mycelium inhabited mainly. Colony: small mycelial mat, Mat: large and thick mycelial mass forming the specific layer, Strand: undeveloped rhizomorph, Rhizomorph: developed rhizomorph with the organized internal structure. Ecto: ectomycorrhiza, Endo: endomycorrhiza.

Habitat	Mycelium in soil	Mycorrhizal fungi	
		host	mycorrhiza
L	Colony transparent		
L	Colony white		
F-H wet	Colony transparent		
F	Rhizomorph white	*Betula*	Ecto white pinnate
F-H	Rhizomorph white	*Betula, Abies*	Ecto white pinnate
F-H	Mat gray thick	*Tsuga, Abies*	Ecto white pinnate rod
F-H	Mat transparent	*Tsuga, Abies*	Ecto yellow pinnate
F	Rhizomorph brown	*Tsuga*	Ecto gray short pinnate
F	Rhizomorph white	*Tsuga*	Ecto white coralloid
F	Rhizomorph white	*Tsuga*	Ecto white coralloid
F-H	Mat gray thick	*Tsuga, Abies*	Ectoendo gray rod
F-H	Mat gray thick	*Tsuga, Abies*	Ectoendo gray rod
F-H	Strand white yellow	*Tsuga*	Ecto yellow pinnate
H	Rhizomorph white	*Betula*	Ecto white pinnate
H	Mat? transparent	*Tsuga, Abies*	Ectoendo brown pinnate
F-H	Rhizomorph yellow		
wood	Mat white		
L2, F4, FH8, H2, wood 2	Colony 3, Mat 6, Rhizomorph & strand 7		Ecto 9, Ectoendo 3

L	Colony transparent		
L	Colony whitish gray		
F-H	Colony transparent		
wood	Colony white		
wood	Mat white thick		
F-H wet	Colony transparent		
F	Rhizomorph yellow	*Betula*	Ecto white pinnate
F	Rhizomorph white	*Betula*	Ecto white pinnate
F-H	Rhizomorph white	*Betula, Abies*	Ecto white pinnate
F-H	Rhizomorph white	*Betula, Abies*	Ecto white pinnate
H	Mat gray thick		
F-H	Rhizomorph white	*Betula*	Ecto white short rod
F-H	Rhizomorph white	*Betula*	Ecto white pinnate
F-H	Strand white long	*Betula, Abies*	Ecto white pinnate
L2, F2, FH6, H1, wood 2	Colony 5, Mat 2, Rhizomorph & strand 7		Ecto 7

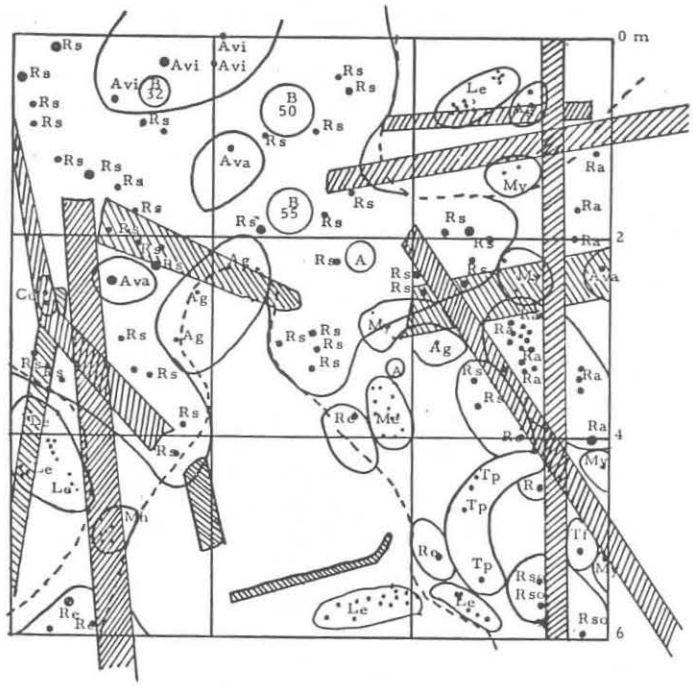

Fig. 4. Occurring positions of sporocarps of higher fungi and their apparent occupied areas in *Betula ermani* and *Abies mariesii* stand.

Sporocarps of higher fungi were collected from plot 2 in 1970. Fungal species names and their marks on the map are listed up in Table 3. B: *Betula ermani* and A: *Abies mariesii* with the breast height diameter in cm.

total dry weight of them 198.5 g. The sporocarps of *Leotia lubrica* and *Russula senecis* were abundant, and the dry weight of the latter reached to 138 g. *Russula aurata, Amanita virosa* and *A. vaginata* exhibited high productivities in weight. The area occupied by the fungal territories was 62% of the plot. The occupied area of *Russula senecis* was largest, and that of *R. aurata* followed it. The fungal flora in this plot was obviously characterized with the dominancy of *Russula* and *Amanita* species which were growing mainly in F to FH layers with the developed rhizomorphs and the pinnate mycorrhizae on *Betula* root. The formers of mycelial mat except for *Telephora palmata* were absent in such a damp site.

Both saprophytes and mycorrhizal fungi were about 50% of total species number. The inhabitants in F or FH layer were dominant, but most of them were enlarging into the spaces among decaying black leaves or humus by means of rhizomorphs. Rhizomorph or mycelial strand formers were 50%, colony formers 35%, and mycelial mat formers only 15%.

Mycorrhizal fungi formed mycorrhizae on *Betula* or *Abies* root. The dominant

species among them, *Russula senecis, R. aurata, Amanita virosa* and *A. vaginata* occurred under *Betula* trees, and their territories enlarged along the root system. Moreover, their territories were duplicated or mixed with each other because of the formation of developed rhizomorphs.

Also in this plot, the occurrence of sporocarps was not observed in the parts covered with heavy snow for longer term and sometimes flooded in late spring.

Only three species were common to both stands, and the dominant species in each plot were different from each other. The species number and the number of sporocarps in *Tsuga* stand were more than those in *Betula-Abies* stand, but the productivity represented by the dry weight and the total occupied area in the former stand were less than those in the latter. The percentage of mycorrhizal fungi in *Tsuga* stand was more than those in *Betula-Abies* stand, but the species number of saprophytes was more in the latter. Although rhizomorph or mycelial strand formers flourished in *Betula-Abies* stand, the fungi forming mycelial mats or undeveloped strands were dominant in *Tsuga* stand where the F and FH layers kept the lower humidity and the better aeration.

On the other hand, the organic matter layer in *Betula* stand was always very humid and became so anaerobic that the aerobic microbes could not persist. So, it might be natural that only the fungi belonging to the same life type could enlarge their territories in *Betula* stand.

In this area, *Tsuga diversifolia* is able to form various kinds of mycorrhizae with the fungi exhibiting different life types more frequently than *Betula ermani*. Therefore, the territories of each species become narrower, and the productivity of sporocarps per unit area increases in *Tsuga* stand.

The high density of fine roots in surface soil layers becomes generally a cause of the abundancy of mycorrhizal fungi. Such trends were recognized also in these stands. Specially the amount of root in surface layer of *Tsuga* stand was more than that in *Betula* stand.

Although the species numbers of litter decomposers were relatively low in both stands, it was supposed that the rapid progress of litter decomposition in *Betula* stand as shown in the decomposition pattern might be caused partly from the abundancy of saprophytes including the several unidentified species of rhizomorph formers in litter.

It is supposed that the high hydrogen ion concentration and high C/N ratio which seem to be unfavorable for the growth of soil bacteria may become one of the causes for the higher fungi to flourish in these subalpine forests.

The characteristics on fungal flora can be represented by some indicators, the productivity of sporocarps, species composition, the number of sporocarps, the occupied area and so on, but there are some problems to be resolved in future. Actually, after all of the members of a certain fungal community and their ecological characters are listed up adequately, it will be possible to extract the dominant or representative species

from each class of life types and to characterize the fungal community. As in plant ecology, the fungal community will be classified into some types depending on environments, vegetation and climate.

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和 文 摘 要

長野県志賀高原，志賀山麓，標高 1500–1800 m の針広混交樹林において高等菌類フロラの調査と，同地域内のコメツガ，ダケカンバ・オオシラビソ林分における高等菌類の生態とその生息環境に関する調査を行った．

高等菌類子実体の発生は7月から10月にわたり，11月から6月までは雪と凍結または地表水の過剰によって微生物活動がほとんど停止した．採集された菌は121種，内菌根菌62種，腐生性菌57種であった．菌根菌の中で高頻度に認められたものはコメツガ林分ではフサクギタケ，ハイイロヌメリガサ，ショウゲンジ，ヌ